

environment for reptiles that need dry environments for egg development and warmth and sunlight to maintain activity. Reptiles must benefit from consistently warmer temperatures at La Selva and Corcovado, although dry, sunny habitats suitable habitat for reproduction may sometimes be limiting for some species, especially at La Selva. Although Palo Verde's dry, warm environment seems ideal for reptilian growth and reproduction, reptile abundance was higher at Corcovado and La Selva. This could be explained by the size of reptiles inhabiting the respective sites. At Corcovado and La Selva, smaller reptiles such as *Basiliscus basiliscus* and anoles (*Norops* sp.) comprised much of the abundance, while many of the reptiles found at Palo Verde were larger species such as iguanas and ctenosaurs. Thus, the number of reptile individuals might not be indicative of the reptile biomass at each site. Understanding factors that influence the diversity and abundance of amphibians

and reptiles is fundamental to understanding their role in communities and ecosystems, and essential in managing landscapes to maintain herpetofauna diversity. Amphibians, due to their reliance on water for reproduction, and reptiles, because of their need for particular temperatures and moisture levels, may be good indicators of environmental change.

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## COMMUNITY PATTERNS IN FLOWER MORPHOLOGY AMONG FOUR TROPICAL FORESTS IN COSTA RICA

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**Abstract:** Pollinator communities could influence the pattern of floral morphology within a community, and floral morphology could influence the structure of pollinator communities. We measured 8 morphological characteristics of flowers representing 11 to 32 plant species of four forests within Costa Rica. Principal components analysis explained 72% of the total variation with axes that were interpretable as size (PC I) and tubularity (PC II). These synthetic measures of morphology differed across sites, flower color classes, and plant families. This suggests that differences in pollinator communities across sites in Costa Rica may influence community patterns in flower size, shape, and color. Any factors that affect the plant community, or pollinator community, are likely to indirectly affect the other because of the strong evolutionary and ecological interactions between flowering plants and animals that visit flowers.

**Key Words:** angiosperm, flower phylogeny, pollinator, plant-animal mutualism

## INTRODUCTION

Many flower-pollinator mutualisms are tied to the evolutionary diversification of angiosperms (Begon 1990). The evolution of flower-pollinator relationships is usually presumed to be the result of reciprocal selective pressures exerted upon one another by both plants and pollinators (coevolution). However, contemporary communities of plants and pollinators are also influenced by ecological processes such as population growth and local extinctions. Sympatry between populations of plants and pollinators could be the result of (1) animal populations evolving and/or persisting based on the presence of plants that provide appropriate floral resources, and/or (2) plant populations evolving and/or persisting based on the presence of animals that provide pollination services. Thus, pollinator communities may be organized around plant communities or plant communities may be organized around animal communities.

The flowers of Costa Rica are ideal for studying flower-pollinator relationships because many plant species in the tropics require outcrossing for reproduction and animal pol-

linators for outcrossing. Flower size, shape, and color may be crucial in attracting pollinators. Pollinator abundances can vary dramatically over small geographic ranges, and the distribution of flowers may follow similar patterns. We hypothesized that there is a non-random distribution of floral morphology across four unique sites in Costa Rica: Corcovado and La Selva, two lowland tropical rain forests, Palo Verde, a tropical dry forest, and Monteverde, a sub-montane tropical cloud forest. For example, red flowers may dominate in one site because the potential pollinator community is composed primarily of hummingbirds. If confamilial flowers located in two different sites are sized and shaped differently, this would suggest that closely related species have evolved in response to differences in pollinator communities across sites.

## METHODS

Floral morphology measurements were collected at four sites in Costa Rica: Palo Verde National Park, Monteverde National Park, Cuerici Biological Station in Cerro de la

Table 1. Results from principal components analysis on 8 morphological characteristics of flowers in four tropical forests. Loading scores indicate the direction and relative contribution of individual characteristics to the principal components axis. Cumulative percents describe the amount of variance explained by the PC axes.

Characteristic	PC 1 Loading scores	PC 2 Loading scores
Corolla diameter	0.39	-0.07
Percent fusion	0.08	-0.29
Stigma-corolla distance	0.29	0.56
Anther-corolla distance	0.29	0.57
Anther-stigma distance	0.31	0.20
Corolla-nectary distance	0.38	-0.38
Stigma-nectary distance	0.47	-0.19
Anther-nectary distance	0.46	-0.23
Cumulative percent	50.2	71.7

Muerte, and La Selva Biological Station, Costa Rica on 12 January, 21 January, 3 February, and 14 February 2000, respectively. At each site, we spent one morning searching for flowers within the primary and secondary forests, and measured one representative inflorescence from as many species as time permitted (about 5 hours). We measured 8 morphological characteristics and recorded 23 other attributes of each species (see Appendix 1 and 2 for complete listing of recorded flower characteristics).

We employed a principal components analysis of eight morphological characteristics of flowers: maximum corolla diameter (mm), percent perianth fusion, minimum stigma-corolla distance (mm), minimum anther-corolla distance (mm), minimum anther-stigma distance (mm), corolla-nectary distance (mm), stigma-nectary distance (mm), and anther-nectary distance (mm) to derive two independent synthetic morphological variables (PC I and PC II). All variables except percent perianth fusion were log transformed ( $\log_{10}(x + 1)$ ) to improve normality. The PCA analysis included one observation of each species at each site, except that species with imperfect flowers were excluded because not all morphological measurements were applicable. We interpreted the first two

principal component scores in our analyses, and used ANOVAs to test for differences among sites, flower color, and family on the first two principle components.

#### RESULTS

Based on the loading scores of the floral measurements in the PCA, we interpreted PC I as an indicator of flower size and PC II as an indicator of flower tubularity (Table 1). Flower size (PC I) differed among four sites (Fig. 1), four flower colors (Fig. 2) and seven families (Fig. 3). Tubularity (PC II) also differed among sites (Fig. 1-3).

Corcovado was represented by larger and more tubular flowers, while La Selva was represented by relatively more medium sized, non-tubular flowers. Flowers at Monteverde and Palo Verde had similar morphologies, ranging from small to medium sizes, and average tubularity. Corcovado and La Selva were comprised of many red flowers, while flowers at Monteverde were both red and white, and flowers at Palo Verde were mostly white and yellow. Among the families occurring at multiple sites, Asteraceae, Marantaceae, Melastomataceae, and Passifloraceae appeared to have slight differences in size and shape between confamilial

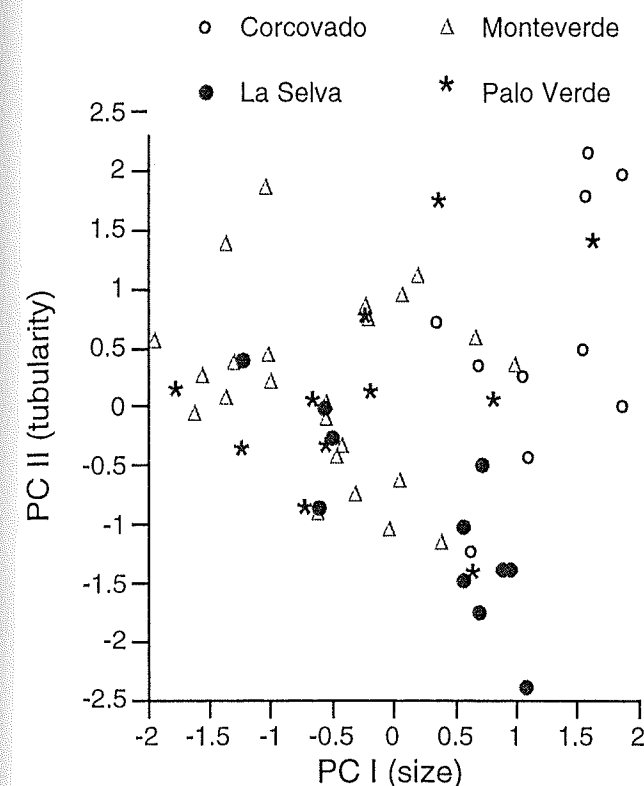


Figure 1. Distribution of flower morphology (as explained by the first two axes of a principal components analysis) in the forest communities of Corcovado, La Selva, Monteverde and Palo Verde, Costa Rica. There were significant differences among sites in PC I ( $F_{3,55} = 12.69$ ,  $p < 0.0001$ ), and PC II ( $F_{3,55} = 6.73$ ,  $p = 0.0006$ ).

species located in the different sites. Co-occurring families tended to be grouped in size and shape at Corcovado, La Selva and Palo Verde. The co-occurring families at Monteverde encompassed a wider range of size and tubularity than the other sites.

#### DISCUSSION

Differences in floral morphology among sites suggests that site-specific pollinator assemblages may have driven the diversification in floral morphology. The large, tubular flowers that dominated in Corcovado may reflect the presence of large pollinators with long tongues or beaks. The medium, moderately-tubular flowers which at Monteverde and small to medium flowers at

Palo Verde, suggest the presence of a more diverse assemblage of pollinators, who vary in body size and often lack long tongues or beaks.

Differences in flower morphology by color class and family may also have resulted from differences in pollinator assemblages. The dominance of red flowers at Corcovado and La Selva suggests a rich hummingbird community at these sites. The dominance of red and white flowers at Monteverde suggests that Monteverde's pollinator community includes many hummingbirds and bats. The white and yellow flowers at Palo Verde may be particularly attractive to moths and various diurnal insects, respectively. Confamilial flowers seem to have diverged between sites. However, a modified sampling technique that provides intensive sampling of a few families at each site would provide stronger tests for pollinator-driven diversification of flower morphology.

Our study supports the theory that pollinator communities have been important in influencing community patterns of floral morphology. However, this relationship is almost certainly not unidirectional. The relative strength of flower morphology and pollinator community probably differs between environments due to both physical and biological attributes of the region. Any factors that affect the plant community of a forest, or the pollinator community, are likely to indirectly affect the other because of the strong evolutionary and ecological interactions between flowering plants and animals that visit flowers.

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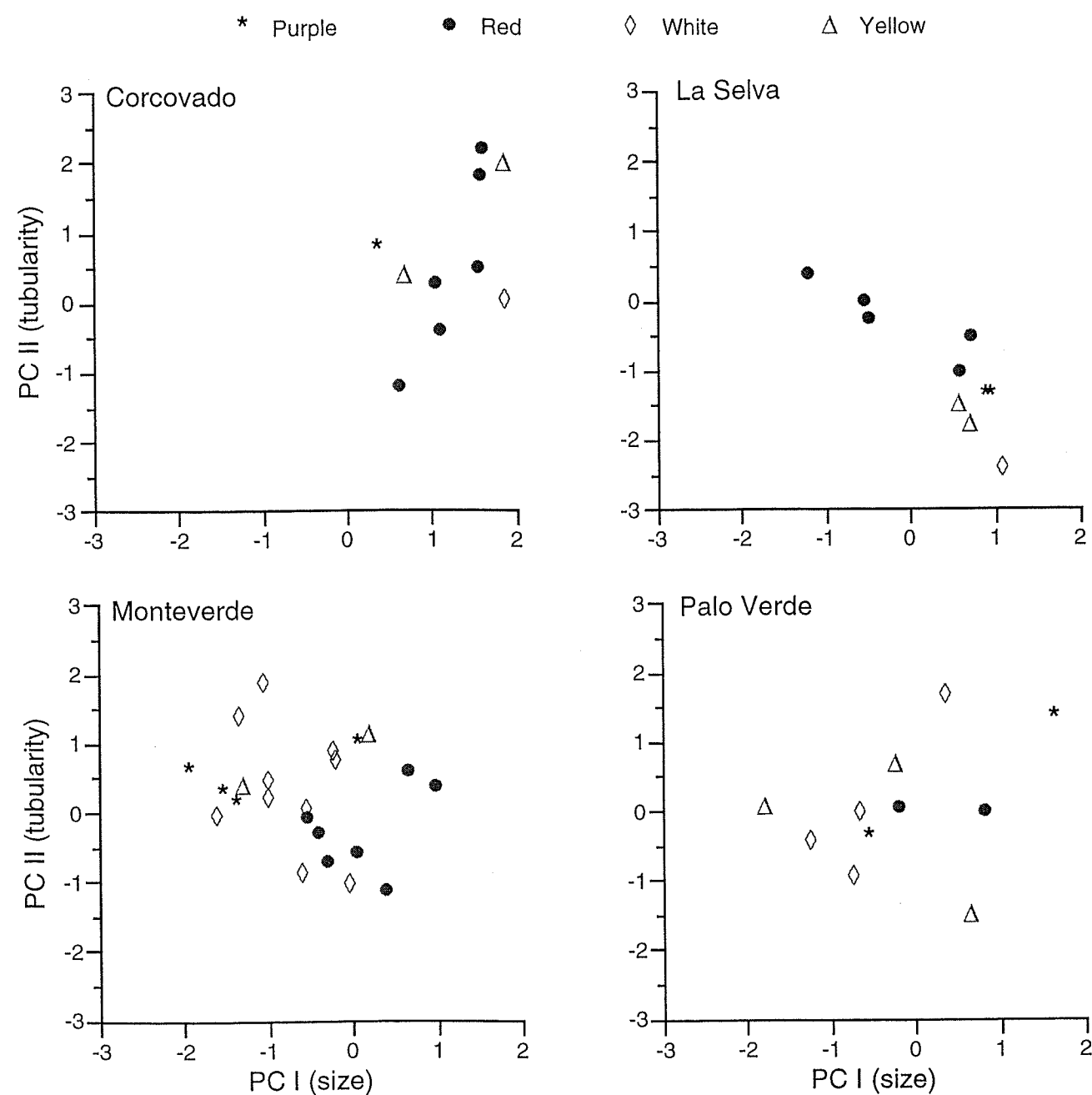


Figure 2. Patterns of flower morphology by color att, four sites in Costa Rica: Corcovado, La Selva, Monteverde and Palo Verde. The effect of flower color on PC I was marginally significant ( $F_{3,53} = 2.30$ ,  $p = 0.088$ ), and non-significant for PC II ( $F_{3,53} = 0.05$ ,  $p = 0.987$ ).

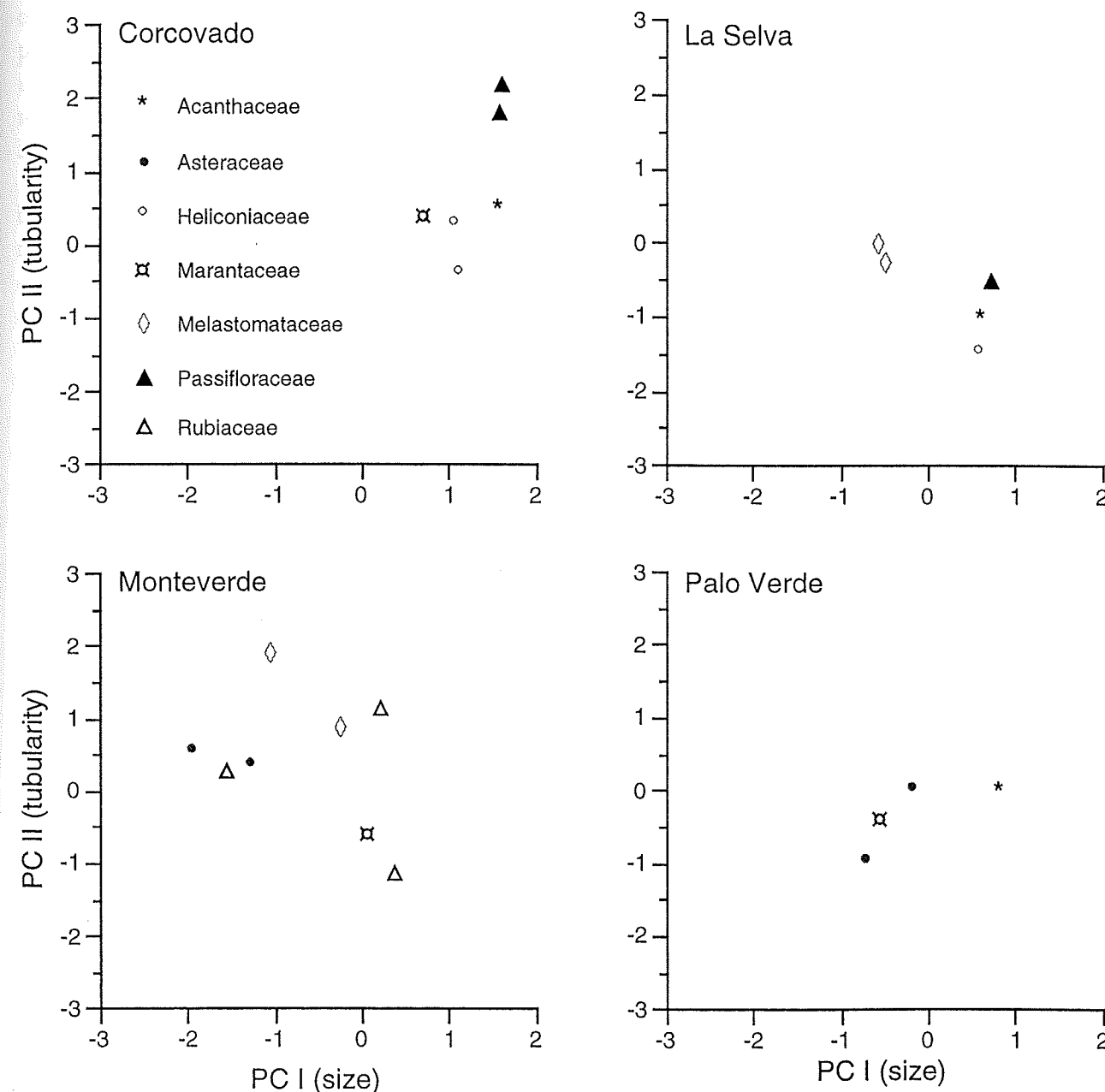


Figure 3. Pattern of flower morphology by family at four sites: Corcovado, La Selva, Monteverde, and Palo Verde. The effect of family on PC I was significant ( $F_{6,24} = 10.06$ ,  $p < 0.001$ ), but the effect on PC II was not ( $F_{6,24} = 1.37$ ,  $p = 0.279$ ).